BOTANICAL GAZETTE

APRIL, 1895.

Present problems in the anatomy, morphology, and biology of the Cactaceæ.

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In this paper I purpose to discuss briefly the subject outlined by the above title, pointing out in particular those questions which can be settled only by study in the field, as well as those which require specially-collected field-material for their solution in the laboratory. The subject can be the more clearly understood and its importance the better judged if I give first a brief description of the anatomical, morphological, and biological characteristics of the family, and then add a short account of progress to our present state of knowledge.

The Cactaceæ form a sharply-defined, although phylogenetically very new, practically entirely American order, including some 1,000 usually badly-defined species grouped in some twenty worse-defined genera. Taken as a whole they exhibit a more extreme deviation from the normal in habits, and therefore in structure, than is to be found in any other large family of flowering plants; they offer in consequence many inviting problems, and as well an unusually favorable opportunity to test some of the great principles which are concerned with the nature of adaptation and the dynamics of development.

For the most part the Cactaceæ are dwellers in the desert and therefore economizers of water. To store water and to protect it from evaporating under the too-great power of the sun, requires a condensed form and this characteristic dominates throughout the order, showing its traces even in those species which have abandoned the desert habit. Containing often the only water-supply upon the desert, they are particularly liable to destruction by thirsting animals, and protection against them explains the presence of the nearly universal spines, the second marked characteristic of the order.

The roots, protected somewhat from the extreme conditions prevailing above ground, have not been found to show notable peculiarities. They often run very deep, are often tuberous for water-storage, are rarely aerial. But in the shoot the necessity for condensation, i. e., for surface reduction in proportion to bulk, has operated to lessen, even to the point of suppression, the branching and leaf-formation, has brought about very special form-conditions, probably unique relations of stem, leaf and axillary bud, and a very finely-adapted series of water-holding tissues.[1]

As to the tissues, it is enough here to say that the characteristic xerophilous appearances are a strong cuticle, thick epidermis, perfect cork, sunken stomata; collenchymatous hypoderma; deep palisade layers; great development of pith and cortex which consist of large round splendidly pitted water-storing cells, often containing mucilage; a fibro-vascular system in general simple in its make-up, lacking annual rings, composed as to its xylem part of strongly ringed and spiralled tracheids which are often collected into gland-like masses, the whole system conforming closely to the external form and following its morphological changes.

In external form, there is every variation from the leafy shrubby Peireskia to the ribbed columns of Cereus, the flat joints of the Platopuntiæ, the phyllocladia of Epiphyllum, or the tubercled spheres of Mamillaria, and everywhere are clusters of spines, in definite relation to which arise the flowers and new branches. How is this medley of structures to be brought into homology with the ordinary stem and leaf condition of other flowering plants? Happily these questions have been mostly solved. All Cactaceæ have leaves which show instead of the ordinary division into blade, petiole, etc., a division into blade and swollen base flattened to the stem.[2] The blade may persist for a season as in Peireskia, fall away early as is usual in Opuntia, remain very small as in Cereus, or microscopic as in Mamillaria. The axillary bud develops, not strictly in the axil, but upon the leaf-base, having been

[1] I am in the agnostic stage on the subject of the nature of the development of adaptations, but I retain the teleological phraseology for its convenience.
For the latter reason also I retain a distinction between anatomy, morphology, and biology, though I know they are not three branches of inquiry, but three phases of one, the first asking what a structure is, the second by what steps it has come to be what it is, and the third why it is what it is.

[2] A xerophilous characteristic, found also in Euphorbiaceæ and others.

forced to this position doubtless as a result of condensation of leaf-bases at the vegetative point. Leaf-base and axillary bud grow henceforth as one structure together and form the tubercle which attains its highest form in Mamillaria and Leuchtenbergia, and numbers of which merging together in vertical rows, sometimes with the cooperation of the stem added, form the ribs of the ribbed forms. Tubercle and rib physiologically replace the lost leaves, and varying in height and form allow of adaptive increase or decrease in spread of green surface, which is all in the xerophilously advantageous vertical direction. The spines are metamorphosed leaves, originating dorsiventrally on the sunken hair-protected axillary vegetative points, which may either be carried up entire by the growth of the tubercles and come to stand finally on their tips, as in Opuntia, Cereus, Echinopsis, Leuchtenbergia, etc., or they may split into two parts as in some divisions of Echinocactus and Mamillaria, one part going up on the tubercle and producing spines, the other remaining behind in or near the axil to produce a flower or a branch.[3] The flowers, produced rapidly during or at the close of the rainy season do not share the vicissitudes of the stem, and show no special adaptations to the dry climate. The ovary is deeply sunken in the flower-bearing stem, and the fruit, though often dry, is usually an edible berry, ensuring the best method of dispersal and conditions for germination in a dry climate. The seedlings are also succulent, with a spread of surface corresponding in a general way to that of the adult plants.

I have elsewhere traced briefly the steps by which this knowledge has been won.[4] The only work upon the comparative anatomy of the order is Schleiden's celebrated treatise of 1845,[5] which despite some errors peculiar to that time, clearly outlined the essential features of the subject. Von Mohl studied their bundle-systems, and many later students have gone to them for special points, all of which may be traced in the work of DeBary,[6] since which little of importance has appeared, for the golden age of anatomy is not in

[3] The full discussion of the points here outlined may be found in my paper, "Beiträge zur Kenntniss der Morphologie und Biologie der Cacteen" in Flora, Ergänzungsband, 1894.

[4] Flora, loc. cit.

[5] For titles, etc., see Flora, loc. cit.

[6] Comparative Anatomy of Phanerogams and Ferns.

these days. As to their morphology most systematists have given it some, though usually it has been scanty attention. De Candolle appears to have begun the attempt to determine the homologies of spine and tubercle and the other riddles of the group; various others, including Kauffmann, Vöchting, Schumann and Wetterwald, and above all Goebel, have debated point after point, and gradually won the truth. Finally I must be permitted to mention my own studies which in ground well prepared by my predecessors were made productive under the guidance of my teacher Goebel. It remains to mention the sources of our knowledge of their biology, and here we have but a single source to refer to, the groundwork for all future studies of this character, Goebel's discussion of their form, protection, and other conditions in his "Pflanzenbiologische Schilderungen."

So much for the characters of this attractive family and the pioneers in its study. What now remains for other explorers?

There is needed first and most important of all, an exact investigation into the meteorological and biological conditions under which the Cactaceæ live. An all the year round study of the amount and time of rainfall, dew-formation, dryness of the air, winds, extremes and means of day and night and seasonal temperature,[7] intensity and amount of light, the kinds and habits of enemies and of cross-pollinating and disseminating friends, the exact situations in which they grow and the nature of the soil, all these must be known about any given district before we can more than guess at the "adaptations" in the Cactaceæ which inhabit it. Excepting for some incidental study by Goebel in Venezuela and the work of Stahl in Mexico last summer, the results of which we have yet to learn, no trained biologist has worked upon them in the field.

Taking first the simpler problems, there are several in which additional evidence is to be expected. It has been clearly shown that the spines of the Cactaceæ are metamorphosed leaves, and not "emergences" as some have claimed. The evidence is drawn from the occurrence of normal transitional structures which are formed by the axillary vegetative points as they begin to sprout into branches, i. e., after they

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[7] The only data of this kind are those given by Coville (Contrib. Nat. Herb. **4**: 33-35. 1894), and these are scanty and for only one locality.

cease to form spines and before they begin to form leaves.[8] These transitions have been found in Opuntia and Echinopsis. Do they occur in other genera? Do they occur on the bases of flower-branches? Do any monstrosities, between leaf and spine, occur?

In the genus Opuntia and confined to it, in addition to the spines, occur the fine barbed bristles, produced on the inner side of the axillary vegetative point. Transitions between these and the spines are to be found on old sprouts of some Opuntias and the two are doubtless homologous. Are transitional forms elsewhere to be found?

The spines of many forms are white in color and weak in texture, even to becoming hair-like as in *Pilocereus senilis* and many others. The epidermal cells of such spines are usually provided with openings through which water may be seen under the microscope to be eagerly absorbed, the air causing the whiteness being expelled, but no trace of a tissue for conducting such water to the living parts has been found. Why do the epidermal cells absorb water? Is it conducted into the stem? The spines of Echinocactus species show a marked cross-banding, due to alternation of clearer and opaquer bands, the former being of larger diameter than the latter. The microscope shows that the cell-cavities in the darker bands contain air, while the clearer lack it. This seems to be an incidental growth condition. Upon what does it depend? What relation do the bands bear to the age of the spine? In the Cylindropuntiæ, each spine is commonly covered by a thin easily separable sheath. This has been found to consist morphologically of a layer of hairs grown together.[9] It cannot be necessary to protect the spine in its development, for others grow equally well without it. Is it of use or was it formerly of use? Is it a growth phenomenon? In some Mamillarias the epidermis of the spines extends out into hairs so that they become feather-like, and this is the common form for them in the seedlings throughout the family. Why are they of this form? Do they help to prevent evaporation?

Very little is known of the biology of the spines. It is assumed that the strong ones protect the plants against animals

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[8]These may be found only when the branches are very young, indeed just as they first show signs of appearance, for the transitional leaf-spines wither and fall off very early.

[9]The discussion of this together with the other topics here mentioned may be found in my above cited paper in "Flora."

and that the bristles, easily separable, rankle in flesh the of an enemy and impress its memory with the dangerous character of that plant. But what purpose do the hooked ends of the spines so commonly found serve? Do they tear rather than prick an enemy? The spines show a great variety of arrangements; are these adaptive to the mode of attack of enemies? Very often there is a strong central spine pointing downwards, suggesting that it is to prevent a hoof from overturning the plant. In other cases, as in *Echinocactus hypacanthus* it points upward, suggesting that the plant may grow in hollows. In very many cases, as in Leuchtenbergia, species of Opuntia, and others, the spines become flat and papery and useless for protection. Of what use are they? In other cases they become flexible hairs. What useful end do they then serve? Is it possible that the strong protective spines occur upon the less extreme desert forms which live where large animals roam, and that these become hairs in the extreme deserts or elsewhere where enemies are rare and need for protection from loss of water is greater? In fact, do hairs and hair-like spines help materially to prevent such loss? Or may it not be that they reflect and refract the too intense rays of the sun and mitigate its force for the green tissues?[10] Can a line be drawn between the hair-like spines, and the morphologically very different multicellular hairs? In Peireskia, some of the spines serve as hooks for climbing. What other uses and forms of them are found? It is plain that Geddes' ebbing-vitality theory for the origin of spines does not apply in this vigorous group, nor is it likely that they are a direct result of dry climate as Lothelier would have us believe. Nowhere in nature is there a better place to test the dynamics of spine production than in this family.

In the genera Mamillaria, Cereus, Rhipsalis, and Opuntia, species[11] have been found which exude nectar in large clear drops from glands among the spines. These are particularly plain in *O. arborescens*. These glands have been proven to be spines more or less metamorphosed. Do they occur in other genera? The exudation takes place only while new parts are being formed. What is its use? Are ants attracted

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[10]Or as Coville (op. cit.) suggests, they may permit too great radiation on the cold nights.

[11]A list of the known species is given in Flora, loc. cit. Nearly every species of Opuntia I have examined, eighteen in all, showed this nectar secretion.

by it which protect the young growing parts against some creeping tissue-eating enemy?

The spines are believed to originate always strictly dorsiventrally from the vegetative point, thus agreeing with one method of production of leaves. This has been proven only for *Opuntia arborescens*. It is desirable to investigate this point in other species and genera. In Peireskia however the spine-production is nearly radial; in Opuntia it becomes dorsiventral, the large spines being produced upon the outer or leaf side of the axillary vegetative point, and the bristles upon the inner or stem side. The dorsiventrality becomes still more marked in Cereus, etc., where nothing, or only some multicellular hairs, is produced upon the inner side; still more so in those species of Echinocactus where the point splits into two parts, and yet more in Mamillaria where it splits into two parts, which separate entirely. Is there any case in which the outer part of the point in Mamillaria produces its spines radially, or are they all laid down dorsiventrally? That a strong central spine closes the growth, as sometimes stated, is altogether improbable.

In *Peireskia aculeata* a very early splitting[12] of the axillary point has been found, one part remaining upon the leaf base, the other being carried up by the young stem in its growth, an exact reversal of the condition in Mamillaria where, after the splitting, one part remains in the axil and the other is carried out by the growing tubercle. Is this condition found in other species of Peireskia? The lower point normally produces the new branch, but when it is destroyed, the upper one does so. From the descriptions it seems as if the flowers are produced from the upper. Is this true? In *P. aculeata*, it is possible that the axillary bud does not at first stand upon the leaf base as in other genera, but in the axil in contact with both leaf and stem. Is this true? It is difficult to understand how otherwise a part of the axillary vegetative point could be carried up by growth of the stem. The transition from Peireskia to Opuntia is perfectly gradual and there can be no doubt that Peireskia is the nearest of all living Cactaceæ to the original stem-form. In *P. aculeata* and *P. bleo* a single large leaf often appears in the center of the spine mass. It seems impossible that this is formed in any other way than

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[12]This splitting of the point so often referred to, is, I believe, unique in this family. It is not a branching nor a bifurcation, but a division into two parts by the going over of some of its central meristem into permanent tissue.

by the vegetative point forming it from a papilla homologous with those of the spines. If this be so, it is, as Goebel points out, additional evidence of the leaf-nature of the spines. Is it so? Are any intermediate forms between spines and leaf produced between the two, or is the transition sudden? Do these same axillary points, after producing the leaves, again produce spines? If so, the homology of the two would be clear. It is important to find a transition between the splitting points of Peireskia and the non-splitting point often carried up by the tubercle in Opuntia.

Epiphyllum shows phenomena in its flower and branch production which are best to be interpreted as due to a splitting of the axillary or the main points. Does this occur? In Rhipsalis a splitting of the axillary into several secondary points does take place. Splitting of the point is now known in Peireskia, Rhipsalis, Echinocactus, Mamillaria, Anhalonium. Does it occur in any other genera?

Leuchtenbergia principis is the most interesting species in the family. Its tubercles have become almost leaf-like, and its axillary points carried up upon their tips so that both spines (here papery) and flowers are produced there. This habit removes it from Mamillaria to that section of Echinocactus in which there is no splitting of the point, but the whole is carried up on the tubercle. Yet Leuchtenbergia is said to put out sprouts from the lower part of the stem. Whence do these come, from purely adventitious bud-formation, or in reality is there a very early splitting of the point, the axillary part remaining a long time latent? The latter is very improbable, but if it occurs it would restore Leuchtenbergia to relationship with Mamillaria. Are the tubercles shed like leaves? The development of this plant is unknown, and will give interesting results.

The tubercles seem generally to act as assimilating organs, and their spread of green surface is readily controlled in amount by varying their height. In Opuntia, as Goebel has lately proven,[13] the production of the tubercle is intimately dependent upon light, not forming at all upon sprouts grown in darkness. He has also shown elsewhere[14] that when the tubercles are protected by a cephalium as in Cephalocereus, and in lesser degree in Melocactus, the union of leaf and ax-

[13]Flora **80:** 96-116. 1895.

[14]Pflanzenbiologische Schilderungen 92, 93.

illary sprout is less extreme than in those which are exposed, but it is a question to just what this is due. Can other cases be found in which tubercles are partially protected or darkened, and what is then their behavior? In flat Rhipsalis species, and some Echinocacti, the backs of the tubercles grow out into papillæ or into wings increasing the spread of surface. In *Cereus rostratus*, these wings are bent backward so that they form hooks enabling the plant to climb, and *C. McDonaldiæ* shows an intermediate condition. Do the tubercles, or the wings from them, serve any other purposes in the family?

In some Echinocacti and Mamillariæ, a deep hair-filled groove unites the spine-bearing and the flower-bearing parts of the split axillary point. This groove is simply the greatly drawn-out sunken area in which the vegetative point is always protected. In the highest *Mamillariæ* however this groove is absent, which is because the splitting of the point occurs before the sunken area, or rather its raised walls, are formed, and each part of the point forms its own wall. *M. macrothele* seems to form an intermediate condition, for the groove is sometimes present, and sometimes not, but in reality it has a groove of which the edges grow together. Are there cases in which the groove persists as a sunken tube? Or are there other transitional forms? The genus Anhalonium though so small has both grooved (*A. fissuratum*) and ungrooved (*A. prismaticum*) forms, a curious case of "parallel-bildung" with Mamillaria, for we cannot suppose that the former came off from the grooved and the latter from grooveless Mamillariæ.[15]

[15] By a very natural mistake in the absence of a study of its embryology, Engelmann and (following him) Coulter have misunderstood the morphology of the tubercles in *Anhalonium*, and especially in that section of *Echinocactus* which the latter has elevated to generic rank under the name of *Lophophora* (Preliminary Revision of the North American species of Cactus, Anhalonium and Lophophora. United States Dept. of Agr. 1894). In the former, the areola near the tip of the tubercle does represent the spine-bearing areola, (indeed it contains small spines) and it is not simply the closed upper extremity of the tubercle groove. The true morphology of the groove shows that its upper extremity always is the spine-bearing areola. Comparing the forms *Echinocactus* (*Anhalonium*) *Williamsii* and var. *Lewinii* with *Anhalonium* he concludes naturally that the spine-bearing areolæ and entire upper part of the tubercle are gone. In reality spine-bearing and flower-bearing areolæ were never separated, but remain united as in all *Echinocacti* which lack the groove—as for example *E. horizonthalonius*. Moreover small spines are found in the areolæ, which latter of course also produce the flowers. If one simply imagines these spines to grow out and become large, he has a form exactly comparable with *E. horizonthalonius*—particularly with the young forms of the latter (see Engelmann, Collected Works, plate 32). These species of *Lophophora* therefore are *Echinocacti*.

In the formation of the ribs of the ribbed forms, parts of what would be morphologically surface of the main stem, seem to take part, so that the raised pieces between the successive spine-clusters may be stem and not tubercle in their nature. Where is this true and where not? Only the most careful study, as to whether or not the leaves are laid down in actual contact at the vegetative point, can settle the matter.

[*To be concluded.*]

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